

LIFE HISTORY OF THE ISSID PLANTHOPPER
THIONIA ELLIPTICA (HOMOPTERA: FULGOROIDEA) WITH
DESCRIPTION OF A NEW *THIONIA* SPECIES FROM TEXAS

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Abstract.—The life history of *Thionia elliptica* (Germar) in Pennsylvania is outlined and the immatures described and illustrated. This univoltine issid has five nymphal instars, feeds on scrub oak (*Quercus ilicifolia* Wang.), has been collected from blackjack oak (*Quercus marilandica* Muenchh.), and apparently overwinters as eggs. Specimens are recorded from Arkansas, Kentucky, Missouri, North Carolina, and Pennsylvania. Specimens from Texas described by Doering as *T. elliptica* differ in the morphology of the aedeagus and, thus, are described as the new species *T. obrienae* Wilson. On the basis of adult and nymphal morphology, it is suggested that acanaloniid planthoppers, generally accorded family status by North American workers, be treated as a subfamily (Acanaloniinae) of the Issidae following Fennah (1954).

The genus *Thionia* includes 71 species distributed throughout the New World (Fennah, 1965; Metcalf, 1958). Doering (1938) monographed the seven species found north of Mexico. Except for occasional references to food plants nothing is known of the biology of any of the species.

While collecting insects in eastern Pennsylvania, a number of specimens of *Thionia* were found on their host plant, scrub oak (*Quercus ilicifolia* Wang.). Upon detailed examination, these specimens were determined to be *T. elliptica* (Germar) nec. Doering; specimens described by Doering (1938) represent an unnamed species.

The present paper includes a study of seasonal history and descriptions of the male and female, eggs, and the five nymphal instars of *T. elliptica*; description of the new species *T. obrienae* Wilson; and comments on the higher classification of issids and acanaloniiids.

MATERIALS AND METHODS

Field study. *T. elliptica* was first collected in 1984 along Rt. 81 about 5 mi south of Frackville (Schuylkill Co.), Pennsylvania. The site, a moist pitch pine-scrub oak barrens at an elevation of ca. 457 m (1,500 ft), is dominated by a canopy of scrub oak and pitch pine, *Pinus rigida* Mill., and an understory of trailing arbutus, *Epigaea repens* L., wintergreen, *Gaultheria procumbens* L., sheep laurel, *Kalmia angustifolia* L., blueberries, *Vaccinium angustifolium* Ait. and *V. vacillans* Torr. (Ericaceae); red chokeberry, *Aronia arbutifolia* (L.) L. (Rosaceae); sweetfern, *Comptonia peregrina* (L.) J. M. Coult. (Myricaceae); and fly-poison, *Amianthium muscaetoxicum* (Walt.) Gray (Liliaceae).

In 1985 samples were taken from 23 April through 15 August by tapping branches of scrub oak over a shallow insect net and collecting the first 10 individuals en-

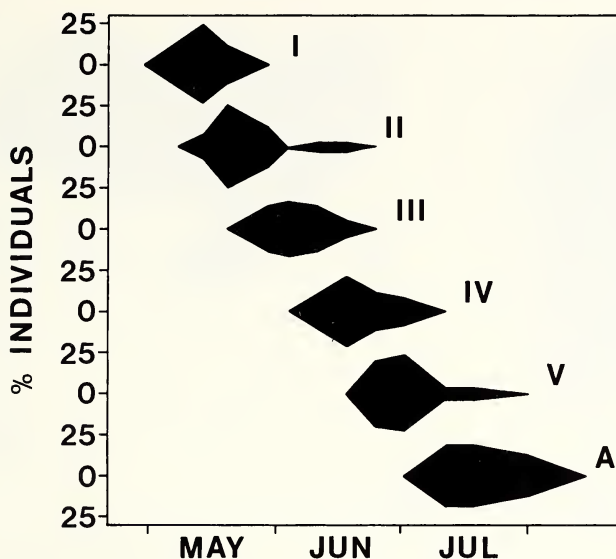


Fig. 1. Seasonal occurrence of *T. elliptica*. Number of individuals of each stage is expressed as percentage of total observations of that stage (I-V = nymphal instars, A = adults).

countered. Collections were made weekly except for a 10-day interval in early July and a 2-week interval in early August. Additional field observations and collections were made at the study site during June–August 1984 and April–September 1986 and in an extensive scrub oak barrens near Long Pond (Monroe Co.), Pennsylvania, in August 1986.

Descriptions of adults and immatures. We attempted to borrow the type specimen of *T. elliptica* that Doering (1938) stated was “according to Melichar in the Museum in Budapest.” In his monograph of the Issidae, Melichar (1906) did not state that the specimen to which Doering referred was indeed at that museum; we assume that Germar’s type has been lost. We were able to borrow a specimen from the Hungarian Natural History Museum in Budapest that corresponded with other specimens collected throughout the eastern United States but not with Doering’s description and illustration based on material from Texas.

Descriptions of nymphs are based on the following field-collected specimens: PENNSYLVANIA: Schuylkill Co., I81 N, 4.5 mi S Frackville (1985 specimens; 1984 specimens = 4.8 mi S), A. G. Wheeler, Jr., Collector, taken on *Quercus ilicifolia* (I–V = nymphal instars, ♂ and ♀ = adults), 21 June 1984 (2-II, 11-III, 3-IV), 27 June (1-II, 6-III, 9-IV, 2-V), 4 July (2-III, 11-IV, 4-V), 12 July (6-V), 14 July (4-III), 19 July (1♂, 1♀), 8 May 1985 (5-I), 14 May (8-I, 3-II), 20 May (4-I, 10-II), 30 May (5-II, 6-III), 4 June (7-III), 11 June (1-II, 6-III, 4-IV), 18 June (1-II, 2-III, 8-IV), 25 June (4-IV, 6-V), 2 July (3-IV, 7-V), 12 July (1-V), 19 July (1-V, 1♂, 1♀), 1 Aug (1♂, 1♀).

Adults were pinned and nymphs preserved in 70% ethyl alcohol. Measurements are given in mm as mean \pm SD. Length was measured from apex of vertex to apex of wings for adults or apex of abdomen for nymphs, thoracic length along the midline

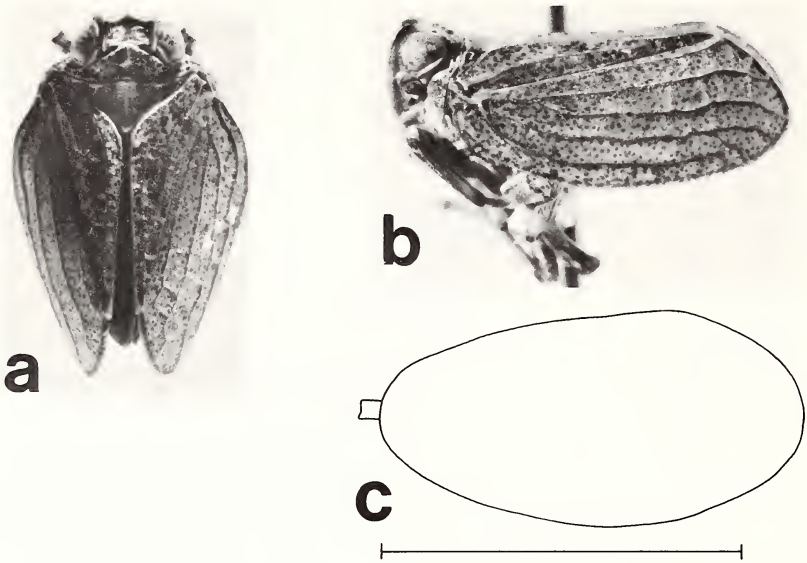


Fig. 2. *T. elliptica*. a. Adult, dorsal view. b. Adult, lateral view. c. Egg, bar = 1 mm.

from the anterior margin of the pronotum to the posterior margin of the metanotum, and width across the widest part of the body. Eggs were obtained by removing them from a dried, pinned female. Eggs were restored by immersion in 10% lactic acid at 80°C for 30 min, fixation in 37% formaldehyde solution for 24 hr, then transference to 70% isopropyl alcohol.

RESULTS AND DISCUSSION

Thionia elliptica (Germar)

Field study. *T. elliptica* is univoltine (Fig. 1) and, based on attempts to collect this issid on white oak, *Q. alba* L., and other trees and shrubs, is apparently limited in its host preference to *Q. ilicifolia* at the study site. However, adult specimens from Missouri, well outside the range of scrub oak, *Q. ilicifolia*, were found on blackjack oak, *Q. marilandica* Muenchh.

In 1985 nymphs were first observed on 8 May when host foliage was beginning to expand. Adults appeared in the sample of 12 July and were collected until 31 July but probably were present until early August; they were absent on 15 August when the next sample was taken (Fig. 1). Seasonal history was similar in 1986. A first-instar nymph was collected on 14 May; adults appeared by 1 July and were present until late August.

This issid probably overwinters in the egg stage, as do acanaloniids and flatids with similar life cycles (Wilson and McPherson, 1981a, b); this contention is supported by the occurrence of a gravid female collected on 19 July 1985 and by the absence of adults in the spring (Fig. 1). Females likely insert eggs in woody tissue as they have teeth on valvulae 2 (Fig. 3e), and the eggs have a sculptured chorion; both

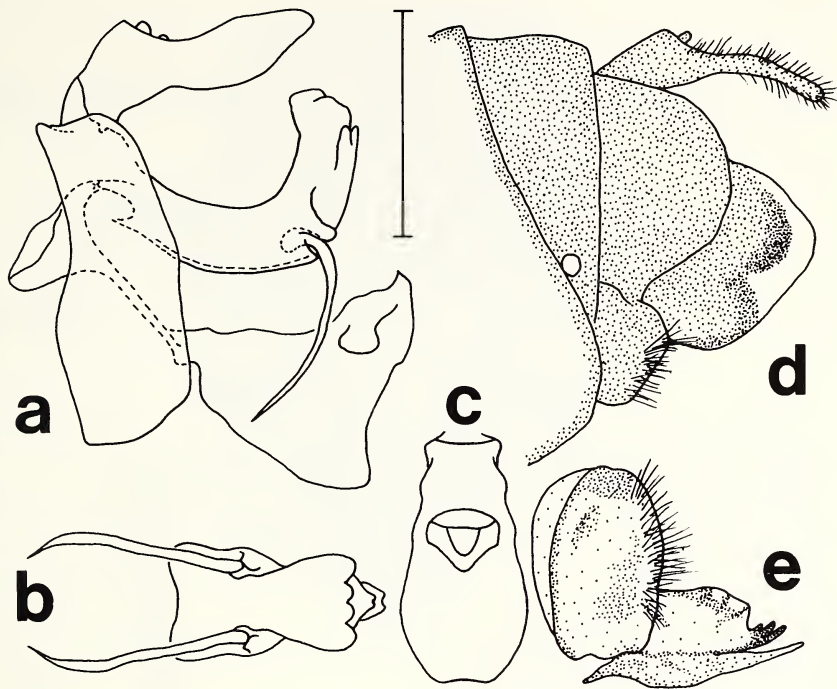


Fig. 3. *T. elliptica* genitalia. a. Male, lateral view of complete genitalia. b. Male, ventral view of aedeagus. c. Male, dorsal view of anal tube. d. Female, lateral view of complete genitalia. e. Female, lateral view of valvula 2. Bars = 1 mm.

features are present in acanaloniids and flatids that oviposit in woody tissues (Wilson and McPherson, 1981a, b).

Nymphs and adults of *T. elliptica* were observed on branches of scrub oak, which appear to be the principal feeding sites on their hosts. This planthopper was consistently beaten from larger branches rather than from the foliage or small branches. A larva of the epipyropid moth *Fulgoraecia exigua* (Edwards) (= *Epipyrops barbariana* Dyar) was observed on the abdomen of a nymph. Wilson and McPherson (1979) listed the known planthopper hosts of this parasitic moth.

Descriptions of adults and immatures. ADULTS (Figs. 2a, b, 3, 7). Length—male 6.2 ± 0.22 ; female 7.2 ± 0.15 ; $N = 10$ for each. Specimens differ from *T. elliptica* as described and illustrated by Doering (1938) in having a wider range of color variation from yellowish and tan to almost black ground color with small dark brown to black spots, smaller size, and different male genitalia.

Male genitalia (Fig. 3a–c). Pygofer, in lateral view, higher than wide. Anal flap, in dorsal view, longer than wide, with a broad, weak apical notch, segment 11 visible near middle as a short ring bearing a stout anal style. Styles (harpagones of Doering (1938)), in lateral view, subtriangular, widest in posterior $\frac{1}{3}$, with lobelike flap extending laterally near dorsoposterior corner. Aedeagus subcylindrical, bearing a scler-

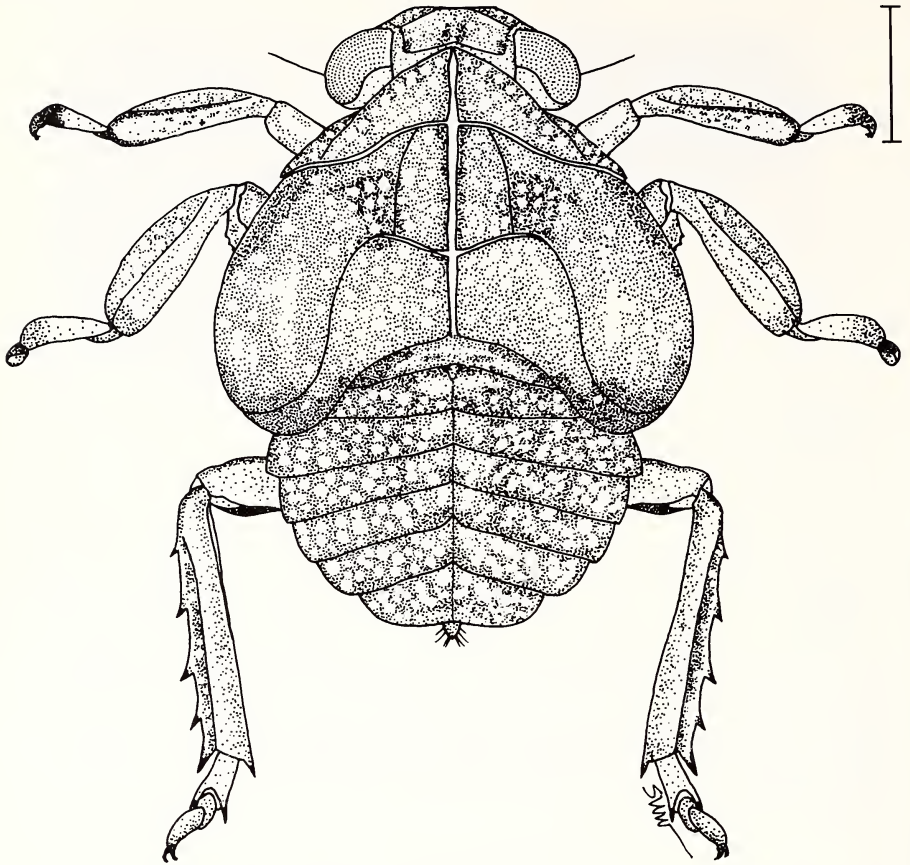


Fig. 4. *T. elliptica* fifth instar. Bar = 1 mm.

otized theca which is difficult to distinguish; in lateral view, theca fully surrounding aedeagus in basal $\frac{1}{2}$, then dividing into dorsal and ventral flaps, dorsal flap extending to apex of aedeagus, with prominent posteroventrally directed lobe posterior to aedeagal process, ventral flap extending nearly to apex of aedeagus, in ventral view, ventral flap with 4 lobes at apex; aedeagus, in lateral view, with an elongate, moveable, curved spinelike process on each side, processes originating in posterior $\frac{1}{2}$ from between thecal flaps and extending posteroventrally; aedeagus, in ventral view, extending beyond theca, apex bilobed.

Female genitalia (Fig. 3d, e). Anal flap spatulate, longer than wide, apical notch weak. Valvulae 1 forming short, covering flaps, subquadrate, heavily sclerotized basal $\frac{3}{4}$ weakly to strongly lobate. Valvulae 2 almost hidden by valvulae 1, apices visible in ventral view, with 3 black apical teeth and slender process originating on ventromedial aspect and extending caudad. Valvulae 3 completely hidden by surrounding valvulae 1 and 2, slender, spinelike, lacking teeth.

Specimens examined. ARKANSAS: Polk, 21 August 1928 (1♂), J. Beamer; Washington Co., 18 September 1939 (1♂, 1♀) (housed in the Snow Museum, University

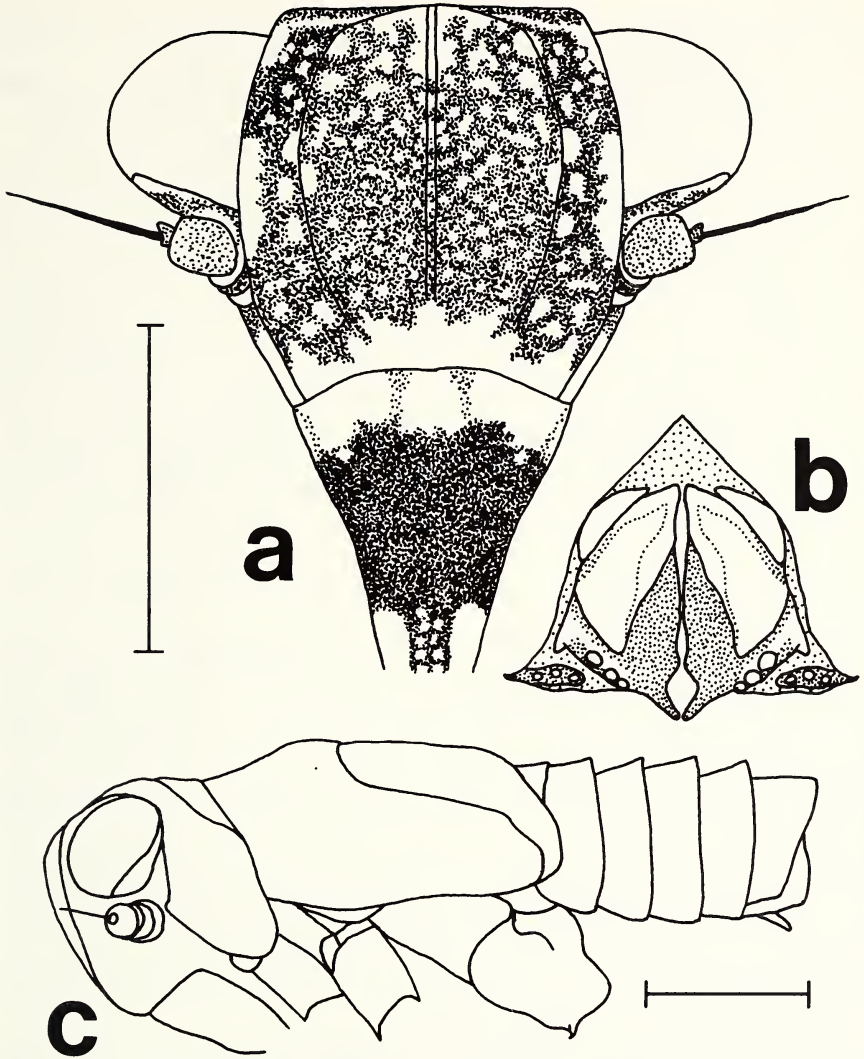


Fig. 5. *T. elliptica* fifth instar. a. Frontal view of head. b. Caudal view of abdomen. c. Lateral view. Bars = 1 mm.

of Kansas, Lawrence); KENTUCKY: Louisville (1♀), with labels "*elliptica* det. Melichar" and "*Thionia elliptica* Germ" (in Horvath's handwriting according to T. Vasarhelyi) (housed in the Hungarian Natural History Museum, Budapest); MISSOURI: Barry Co., 6 August 1949 (1♂), C. Wingo; Boone Co., Ashland Wildlife Area, 3 September 1969, Malaise Hatch 623 (1♀); Columbia, 2 September 1979, E. G. Riley (1♀); Pennicles, 15 mi N Columbia, 1 July 1957, coll. F. W. Wood (1♀); Carter Co., Sky Line Drive nr. Van Buren, 22 July 1978, E. G. Riley (2♂); Crawford Co., 21 July 1972, T. R. Yonke (1♂), 28 June 1974, D. Kopp (1♀), 12 mi E Steelville, 20

August 1980, Coll. E. G. Riley (1♂); Dent Co., 26 July 1973, (1♂); 19 September 1972, 29 July 1973 (1♀), window fl. trap (2♂, 1♀); 12 September 1972 (1♂), 26 July 1973 (1♂), 10 mi E Salem, 2 July (1♂), 19 July (1♀), 26 July 1972 (1♂), 16 August (1♀), 23 August 1972 (1♀), M. P. Roling; Douglas Co., 14 September 1979, R. A. McKinney (1♀); Jefferson Co., Mastodon State Park, 3 August 1982, coll. T. C. MacRae, on *Quercus marilandica* (1♂); Maries Co., 6 mi N Vichy, 10 July 1974, S. E. Thewke (1♂); Phelps Co., Vichy Fire Tower, 2 August 1972, M. Roling (1♂); Reynolds Co., 20 July 1972, M. Roling (1♂); Shannon Co., Loggers Lake RS, 16 July 1983, T. C. MacRae (1♂); Owls Bend, 11 September 1969, L. R. Hanning, on oak leaf (1♀); Stoddard Co., 2 mi SW Bellcity, Ardeola Hill, Crowley's Ridge, 7 July 1979, E. G. Riley (1♀); Texas Co., G. O. White St. Nursery, 3 September 1977, coll. E. G. Riley (1♂); Wayne Co., Williamsville, 7 September 1956, M. Ferril (1♀) (housed in the collection at the University of Missouri, Columbia); NORTH CAROLINA: Black Mts., 15–20 June 1912 (1♂, 1♀), 21–30 June (2♂), Beutenmuller (housed in the collection at Cornell University, Ithaca, New York); PENNSYLVANIA: Monroe Co., Long Pond, A. G. Wheeler, Jr., Collector, taken on *Quercus ilicifolia*, 1 August 1986 (7♂, 2♀); Schuylkill Co., 181 N, 4.8 mi S Frackville, A. G. Wheeler, Jr., Collector, taken on *Quercus ilicifolia*, 19 July 1984 (2♂), 19 July 1985 (1♂, 1♀), 1 August 1985 (1♂).

FIFTH INSTAR (Figs. 4, 5, 7). Length 5.3 ± 1.03 ; thoracic length 2.0 ± 0.11 ; width 3.5 ± 0.29 . $N = 10$.

Form subcylindrical, convex dorsally, slightly flattened dorsoventrally, widest across mesothoracic wingpads; medium brown to black, heavily marked with cream spots.

Vertex ca. $3 \times$ broader than long, anterior margin carinate, subacute, meeting inner carinae of frons medially, lateral and posterior margins weakly carinate. Frons slightly wider than long, dorsal margin nearly straight, lateral margins strongly convex and carinate (outer carinae) paralleled by inner carina on each side, with median longitudinal carina; juncture with clypeus acutely concave; ca. 30 pits, most corresponding with pale spots, between each inner and outer carina. Clypeus consisting of a subconical basal anteclypeus and a subconical distal postclypeus, anteclypeus black with pale at juncture with frons, postclypeus pale with black markings. Beak 3-segmented, extending to metacoxae; segment 1 obscured by postclypeus, segments 2 and 3 subequal. Eyes reddish with pale stripes. Antennae 3-segmented; scape short and ringlike; pedicel ca. $2 \times$ length of pedicel; scape with more than 15 pits; flagellum whiplike distally, bulbous base ca. $\frac{1}{4} \times$ that of pedicel.

Thoracic nota divided by longitudinal mid-dorsal line into 3 pairs of plates. Pronotal anterior margin broadly rounded and carinate, posterior margin sinuate; each plate with 4 irregular rows of pits, totalling ca. 30 pits (lateralmost pits not visible in dorsal view). Mesonotal median length $1.5 \times$ that of pronotum; each plate with carina originating on anterior margin in median $\frac{1}{4}$ and extending posterolaterally to posterior margin; cluster of 9–11 pits just lateral to carina and 6–8 pits on wingpad; wingpad lobate, extending nearly to apex of metanotal wingpad. Metanotal median length ca. $0.7 \times$ that of mesonotum; each plate with weak longitudinal carina originating on anterior margin in median $\frac{1}{3}$ and extending to posterior margin; wingpad broadly lobate, extending laterally to tergite 3. Pro- and mesocoxae elongate, subcylindrical, posteromedially directed; metacoxae fused to sternum. Metatrochanters each with a row of 11 interlocking, flattened teeth on median aspect. Femora slightly

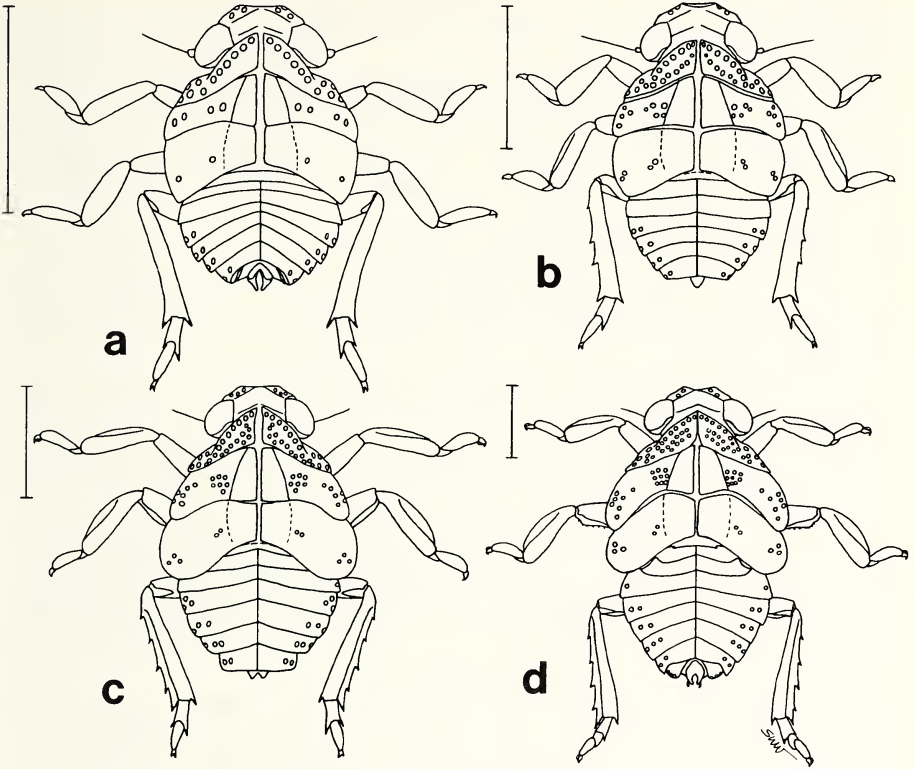


Fig. 6. *T. elliptica* first through fourth instars, a. First instar. b. Second instar. c. Third instar. d. Fourth instar. Bars = 1 mm.

flattened, subtriangular in cross section; pro- and mesofemora shorter and broader than metafemora. Pro- and mesotibiae slightly flattened and subtriangular in cross section, outer aspect strongly concave; metatibiae laterally flattened, longitudinal row of 4–5 lateral spines on shaft and transverse apical row of 7–9 spines (generally 8) on plantar surface. Pro- and mesotarsi each with 2 tarsomeres; tarsomere 1 wedge-shaped, tarsomere 2 subcylindrical and curved. Metatarsi each with 3 tarsomeres; tarsomeres 1–3 subcylindrical; tarsomere 1 with transverse apical row of 8–10 spines (generally 9) apically on plantar surface; tarsomere 2 with 2 spines, 1 on each side, and a large median lobe on plantar surface; tarsomere 3 similar to terminal tarsomere of other legs. All legs with terminal pair of black curved claws and a clear, membranous, lobate, median pulvillus.

Abdomen 9 segmented, subtriangular in cross section, widest across segment 3; segments 8–9 telescoped anteriorly; 7–8 with a pair of elongate, oval, white caudal waxpads. Segment 9 elongate vertically, surrounding anus, with 2 pits and a small fingerlike process on each side; tergites 2–7 with a weak median longitudinal carina. Each tergite with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view due to curving of tergites onto ventral aspect): tergite 3 with 4–5 pits, 4 with 5–6, 5 with 6–7, 6 with 7, 7 with 7–8, and 8 with 5–6.

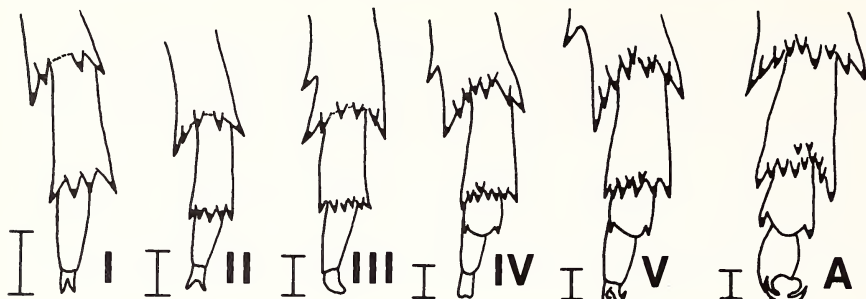


Fig. 7. *T. elliptica* apices of metathoracic legs, plantar surface. I-V = nymphal instars, A = adult. Bars = 0.1 mm.

FOURTH INSTAR (Figs. 6d, 7). Length 5.0 ± 0.53 ; thoracic length 1.6 ± 0.07 ; width 2.3 ± 0.14 . N = 10.

Vertex ca. $3.5 \times$ broader than long. Frons with juncture with clypeus concave and broadly rounded. Antennal pedicel with ca. 12-14 pits.

Pronotal plates each with ca. 27-28 pits in 3 irregular rows. Mesonotal plates each with 6-9 pits just lateral to carina; wingpad broadly lobate and covering ca. $\frac{1}{2}$ metanotal wingpad laterally. Metanotal wingpad with 3 pits in lateral $\frac{1}{3}$. Metatrochanter with a row of 9 flattened teeth on median aspect. Metatibiae with apical transverse row of 7-8 spines (generally 7) on plantar surface. Metatarsomere 1 with apical transverse row of 6-8 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view): tergite 3 with 3-5 pits, 4 with 7, 5 with 5-7, 6 with 5-6, 7 with 6-7, 8 with 3-5; segment 9 with 2-3 pits.

THIRD INSTAR (Figs. 6c, 7). Length 3.6 ± 0.46 ; thoracic length 1.3 ± 0.05 ; width 1.8 ± 0.07 . N = 10.

Frons with ca. 23 pits between each inner and outer carina. Antennal pedicel ca. $3 \times$ length of scape and with ca. 8 pits; bulbous portion of flagellum slightly less than $\frac{1}{2} \times$ length of pedicel.

Pronotal plates each with 21-28 pits in 3 irregular rows. Mesonotal plates each with 6-7 pits just lateral to carina and 5-6 pits in lateral $\frac{1}{3}$. Metanotal plates each with 2-4 very obscure pits just lateral to carina and 3-4 pits in lateral $\frac{1}{3}$. Metatibiae with an apical transverse row of 6-7 (generally 6) spines on plantar surface. Metatarsi with 2 tarsomeres; tarsomere 1 cylindrical, with an apical transverse row of 6 spines on plantar surface; tarsomere 2 similar to terminal tarsomeres of other legs.

Abdominal tergites each with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view): tergite 3 with 3-4 pits, 4 with 4-5, 5 with 5, 6 with 4-5, 7 with 5, 8 with 3-4; segment 9 with 2 pits.

SECOND INSTAR (Figs. 6b, 7). Length 2.6 ± 0.37 ; thoracic length 0.9 ± 0.04 ; width 1.3 ± 0.07 . N = 10.

Vertex ca. $4 \times$ wider than long. Frons with ca. 18-20 pits between each outer and inner carina. Antennal pedicel appearing to have 4-5 very obscure pits.

Pronotal plates each with 20-21 pits in 2 distinct transverse rows. Mesonotal plates each with group of 5 pits just lateral to carina and 4 pits near lateral border. Metanotal plates each with 2 pits just lateral to very weak carina and 1-2 pits near lateral margin.

Metatibia with 3 lateral spines on shaft and an apical transverse row of 5 spines on plantar surface. Metatarsomere 1 with an apical transverse row of 5 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side of midline (lateralmost pits not visible in dorsal view): tergite 3 with 1 pit, 4–7 each with 3 pits, 8 with 2 pits; segment 9 with 2 pits.

FIRST INSTAR (Figs. 6a, 7). Length 1.9 ± 0.29 ; thoracic length 0.7 ± 0.02 ; width 0.9 ± 0.04 . N = 10.

Vertex ca. $3 \times$ wider than long. Frons with 12 pits between each inner and outer carina. Antennal pedicel ca. $2 \times$ length of scape; pedicel lacking pits.

Pronotal plates each with 11 pits in 1 transverse row (along carina). Mesonotal plates each with 2 pits just lateral to carina and 2 pits near lateral margin. Metanotal plates each with 1 pit just lateral to carina and 1 pit near lateral margin. Metatibiae lacking spines on shaft; with an apical transverse row of 4 spines on plantar surface. Metatarsomere 1 with an apical transverse row of 4 spines on plantar surface.

Abdominal tergites each with the following number of pits on either side (lateralmost pits not visible in dorsal view): tergite 3 with 0 pits, tergites 4–7 each with 2 pits, tergite 8 with 1 pit; segment 9 with 2 pits.

EGG (Fig. 2c). Length 1.5 ± 0.03 ; width 0.8 ± 0.01 . N = 3.

Eggs elongate, oval; white (when restored as described in Materials and Methods); chorion translucent, with polygonal sculptured pattern (not illustrated), cephalic end with short cylindrical process.

Thionia obrienae Wilson, new species

Adults. Length—male 6.6 (length from vertex to apex of hindwing; specimen with forewings destroyed; comparable measurement of male *T. elliptica* = 5.6); female 10.0; N = 1 of each). This species differs from *T. elliptica* in its larger size; the male may be separated from *T. elliptica* males by its slightly stouter anal flap, presence of an elongate spine on each aedeagal process, smaller lobe just posterior to origin of aedeagal process, and bilobate rather than quadrilobate apex of theca in ventral view. The female has distinctly larger genitalia, valvulae 1 with heavily sclerotized basal $\frac{3}{4}$ not lobate, and apices of valvulae 2 longer and more strongly curved. *T. obrienae* was described and illustrated, as *T. elliptica*, by Doering (1938:459–460, 542–547, 550–553).

Specimens examined. HOLOTYPE: TEXAS: Concan, 4 June 1933, P. W. Oman, with labels “*Thionia elliptica* (Germ) Det. Doering”, “♂,” “See slide no 69 (F) K. Doering.” “Holotype, *Thionia obrienae* Wilson”; ALLOTYPE: TEXAS: Boerne, 2 July 1936, R. H. Beamer, with labels “*Thionia elliptica* (Germ) Det. Doering,” “♀,” “Allotype, *Thionia obrienae* Wilson.” Types in the Snow Museum, University of Kansas, Lawrence. The species is named in honor of Dr. Lois B. O'Brien, who first suggested that it may be undescribed and who has contributed immeasurably to our knowledge of New World Fulgoroidea.

COMMENTS ON THE HIGHER CLASSIFICATION OF THE ISSIDAE AND ACANALONIIDAE

The higher classification of the Issidae was last reviewed by Fennah (1954) who listed five subfamilies. One of these was the subfamily Acanaloniinae which, both

previous and subsequent to his work, has been recognized as a family, especially by many North American workers (e.g., Muir, 1930; Metcalf, 1958; O'Brien and Wilson, 1985). The family status is based solely on the absence of lateral spines on the metatibiae of adults; all other features given by Metcalf (1954) vary within the family or are also shared with some issids. Certain features of the nymphal morphology do not support the separation of these planthoppers from the issids. Nymphs of *Acanalonia bivittata* (Say), *A. conica* (Say) and *A. latifrons* (Walker) have lateral metatibial spines in the second through fifth instars and have waxpads on the membranous regions of tergites 6–8 (Wilson and McPherson, 1981a; Wilson, personal observation). They are, in fact, quite similar to nymphs of *T. elliptica*, which also have metatibial lateral spines and waxpads associated with tergites 8–9.

In contrast, nymphs of *Acanalonia* and *Thionia* differ greatly from those of the calisceline *Bruchomorpha oculata* Newman (Wilson and McPherson, 1981c), which lacks waxpads. Nymphs of *Acanalonia*, *Thionia* and the flatids *Anormenis*, *Metcalfa*, *Ormenaria*, *Ormenoides*, and *Cyarda* are more similar to each other morphologically than any are to *Bruchomorpha* (Wheeler and Hoebeke, 1982; Wilson and McPherson, 1981a, b, c; Wilson and Tsai, 1984). Scudder's (1979) "Caliscelidae" may indeed have some validity.

Based on nymphal and adult morphology, we feel that Acanaloniidae should be lowered to subfamily rank within Issidae as suggested by Fennah (1954). Phylogenetic analyses of the subfamilies and tribes will be necessary to clarify the relationships and validity of issid higher taxa.

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